

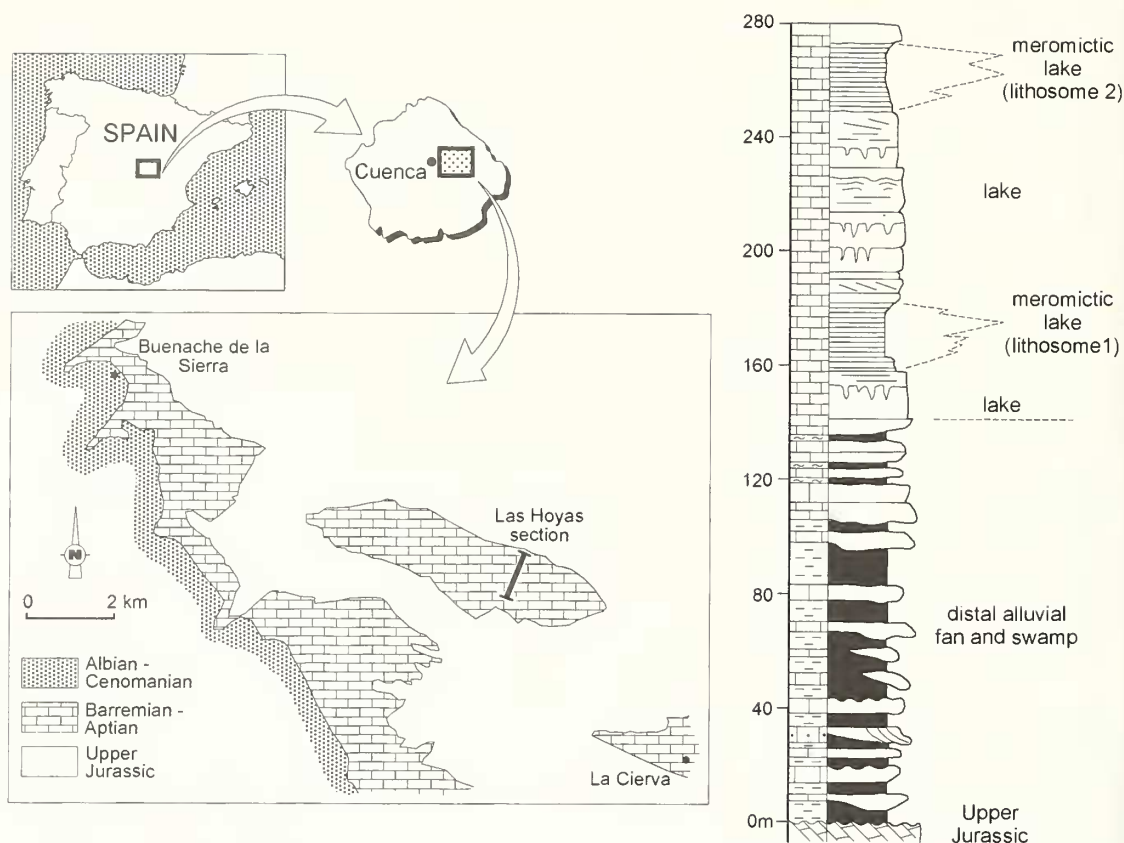
CHAROPHYTES FROM THE LOWER CRETACEOUS OF THE IBERIAN RANGES (SPAIN)

by CARLES MARTÍN-CLOSAS and CARMEN DIÉGUEZ

ABSTRACT. In the Upper Barremian of the Iberian Ranges (Las Hoyas, Cuenca, Spain) an association of exceptionally well preserved charophyte thalli comprises four new form-species: *Palaeonitella vermicularis* sp. nov., *Charaxis spicatus* sp. nov., *Clavatoraxis robustus* gen. et sp. nov., and *Clavatoraxis diaz-romerali* sp. nov. This is the youngest fossil record of the genus *Palaeonitella*. The new form-genus *Clavatoraxis* is erected to include charophyte vegetative remains bearing spine-cell rosettes, a character attributed to the family Clavatoraceae. This is the first time an assemblage of charophyte vegetative remains has been described and related to assemblages of fructifications. This gives a good correlation at family level between the frequency of taxa found as vegetative remains and calcified fructifications. Two biocoenoses are represented: *Clavatoraxis robustus* displays adaptations found in extant charophytes living in permanent shallow water lakes whereas *Clavatoraxis diaz-romerali* was adapted to light-limited, probably deeper, environments. *Palaeonitella vermicularis* grew twisted round thalli of *Clavatoraxis*. Early Cretaceous freshwater communities appear to have been dominated by charophytes, and not by aquatic ferns as believed previously.

CHAROPHYTES include complex green algae, which are considered to be part of the evolutionary lineage leading to vascular plants (Kenrick 1994). The fossil record of these fresh- to brackish-water plants is rich, extends from the upper Silurian to the present, and is composed mainly of calcified fructifications called gyrogonites and utricles. Fossil whole plant remains are extremely scarce. Lower Cretaceous whole plant remains of charophytes consist of silicified specimens from the British Purbeck (Harris 1939), the Morrison Formation of the United States (Peck 1957) and the Barremian of Argentina (Musacchio 1971). Although small fragments of calcified vegetative remains of charophytes are not uncommon in marls prepared for the study of fructifications or in thin sections of lacustrine limestones, this is the first time that a complete association of large vegetative charophyte remains has been found in the post-Palaeozoic fossil record. The study of these fossils is not only necessary to increase knowledge of the morphology of the plants producing the fructifications currently studied, but also enables us description of the structure of an Early Cretaceous freshwater community and underlines the significance of charophytes in subaquatic freshwater environments prior to the radiation of angiosperms.

The material studied consists of exceptionally well preserved charophyte thalli from finely laminated lacustrine limestones in the La Huérguina Formation at Las Hoyas, near Cuenca, Spain (Text-fig. 1). The material was obtained in part by bed-by-bed sampling during the annual excavations of the site and also from the collection of Mr Armando Díaz-Romeral, from Cuenca, who discovered the charophyte remains. Charophyte thalli are calcified and preserved in three dimensions within laminites. In most specimens the surface is slightly corroded. This material was studied directly under light microscopy after immersion in an organic solvent. Limited etching with diluted acetic acid was necessary to prepare some specimens. Thin sections were also prepared to observe the internal anatomy of thalli. Since no three-dimensionally preserved fructifications were found attached to the thalli studied they have been named after already known or newly described form-taxa which are reserved for vegetative remains. A correlation between these taxa and the general systematics of fossil charophytes, which is based exclusively on fructifications, is currently only intended above the suprageneric level. For clavatoracean fructifications the systematics followed agrees with the phylogenetic system of Clavatoraceae proposed by Martín-Closas (1996).



TEXT-FIG. 1. Geographical location and stratigraphical section of the palaeontological site of Las Hoyas; modified from Fregenal-Martínez and Meléndez (1993).

The marls and limestones of the La Huérguina Formation, which include the finely laminated limestones of Las Hoyas, were deposited in the south-eastern Iberian Basin, one of the Mesozoic intracontinental basins of the Iberian Plate. These basins contain up to 5000 m of Late Jurassic to Early Cretaceous sediments as a result of significant basement subsidence related to rifting of the Central Atlantic crust (Álvaro *et al.* 1979; Salas and Casas 1993). The south-eastern Iberian Basin was orientated following the general north-west to south-east trend of the Iberian Ranges. It opened towards the south-east to the Tethys sea, where the deposition of marine shallow water limestones dominated, whereas towards the opposite, north-western end of the basin, the sedimentation occurred mainly in freshwater facies, including the deposition of the La Huérguina Formation (Mas 1981; Meléndez 1983; Fregenal-Martínez and Meléndez 1994). This palustrine and lacustrine unit is up to 280 m thick in the area studied and includes two lithosomes, about 25 m thick, of finely laminated lacustrine limestones separated by palustrine and lacustrine stratified limestones and marls (Fregenal-Martínez and Meléndez 1993). The laminated limestones correspond to the distal, anoxic facies of a meromictic lake (Gómez-Fernández and Meléndez 1991), which preserved floral and faunal remains exceptionally well and provided the charophyte specimens studied here. Biostratigraphical analysis of charophyte and ostracod associations (Diéguez *et al.* 1995a) indicates that this unit is of Late Barremian age.

The fossils found at Las Hoyas include representatives of almost all Lower Cretaceous continental groups. The site has provided significant new taxonomic and phylogenetic data about

fish (Poyato-Ariza 1995), amphibians (McGowan and Evans 1995), dinosaurs (Pérez-Moreno *et al.* 1994) and birds (Sanz *et al.* 1996) along with invertebrates, such as insects (Martínez-Delclòs *et al.* 1995) and crustaceans (Rabadà 1993). Plant fossils are also very abundant and well preserved and include charophytes, bryophytes, ferns, conifers, cycadales, bennettitales, gnetales and early angiosperms (Sanz *et al.* 1988; Diéguez *et al.* 1995b). The enigmatic plant *Montsecchia vidali* (Zeiller 1902) Teixeira, 1954 is also present and constitutes one of the most abundant plant remains. Especially significant for this study is the absence of other freshwater macrophytes apart from charophytes.

SYSTEMATIC PALAEONTOLOGY

Division CHAROPHYTA Migula, 1897

Class CHAROPHYCEAE Smith, 1938

Order CHARALES Lindley, 1836

Form-genus PALAEONITELLA Pia, 1927 emend.

Type species. *Palaeonitella cranii* (Kidston and Lang 1921) Pia, 1927.

Original diagnosis. Vegetative shoot clearly organized in nodes and internodes with whorls of short branches. Reproductive organs so far unknown. Many details of organization are reminiscent of Characeae (Pia 1927, p. 91). ('Deutlich in Knoten und Internodien gegliederte vegetative Sprosse mit wirtelig gestellten Kurztrieben. Fortpflanzungsorgane sind bis jetzt nicht bekannt. Viele Einzelheiten der Organisation erinnern an die Characeen').

Emended diagnosis. Vegetative shoot organized in nodes and internodes with whorls of short, non-branching branchlets. Thallus ecorticate. Reproductive organs so far unknown.

Remarks. The ecorticate thallus of *Paleonitella* is the main character to separate this genus from other post-Palaeozoic form-genera such as *Charaxis* Harris, 1939. The absence of furcations in branchlets of *Palaeonitella* distinguishes this genus from the Devonian ecorticate genus *Octochara* Gess and Hiller, 1995. Thalli of another Devonian genus, *Hexachara* Gess and Hiller, 1995, are similar in organization to *Palaeonitella* but the laterals of the former should be termed bract-cells since they always bear large gyrogonites.

Palaeonitella vermicularis sp. nov.

Plate 1, figures 1–4

Derivation of name. The name refers to the flexible and filamentous aspect of the thalli, which resemble worms (Latin, *vermis*).

Holotype. Specimen LH-16100 from the collection of Mr Armando Díaz-Romeral, Museo de Cuenca (Cuenca, Spain), deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.

Paratypes. Specimens LH-1319 and LH-16102 (the latter from the collection of Mr Armando Díaz-Romeral), Museo de Cuenca (Cuenca, Spain), deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.

Type layer and locality. Second lithosome of finely laminated limestones of the La Huérguina Formation at Las Hoyas (Cuenca, Spain).

Material. Specimen LH-16100 is an assemblage of abundant thalli, which are difficult to individualize. Specimens LH-1319, LH-16102, LH-16103 and LH-16104 contain individual portions of thalli.

Diagnosis. Extremely fine filamentous and flexible ecorticate thalli with nodes bearing about twelve, 1–2 mm long, single-celled branchlets and internodes separated at intervals of 1.5–3.5 mm.

Description. Charophyte vegetative remains flexible and filamentous in overall aspect, ecorticate and poorly calcified (Pl. 1, figs 1–2). Nodes bear about ten (probably 12) small (1–2 mm long) single-celled branchlets and are separated by ecorticate internodes, which lack a cortex of cells (Pl. 1, figs 3–4). Internodes 1.8–3.2 mm (mean 2.3 mm) long and 0.2–0.8 mm wide. No fructifications have been found attached to these thalli.

Comparisons. *Palaeonitella cranii*, from the Devonian Rhynie Chert, Scotland (Kidston and Lang 1921; Pia 1927), differs from *P. vermicularis* in its smaller size (relative difference 1:10) and possession of noded branchlets (single-celled in *P. vermicularis*). The other species described within the genus, *Palaeonitella tarafiyensis* Hill and El Khayal, 1983, from the Upper Permian of Saudi Arabia, is similar in general size and structure of branchlets to our material. However, the internodes of *P. tarafiyensis* are extremely long (up to 25 mm) and nodes are swollen to about twice the width of internodes, whereas in *P. vermicularis* internodes are short and nodes have about the same width as internodes. The Permian species appears much more rigid than the Cretaceous species, in spite of the similar preservation as lime-encrusted fossils.

Remarks. *Palaeonitella vermicularis* is relatively common in the samples studied and is associated with *Clavatoraxis robustus* and *Clavatoraxis diaz-romerali*. On the basis of the ecortication of *Palaeonitella* it has traditionally been accepted that this form-genus is reminiscent of extant Characeae Nitelleae. However, extant representatives bear furcated branchlets, unlike *Palaeonitella*. On the other hand, some Characeae Chareae are also ecorticate, and this may have been the condition of many other taxa which are exclusively fossil, such as the Devonian genera *Octochara* and *Hexachara*. Therefore, at present, assignment of *Paleonitella* to Nitelleae is a hypothesis.

Paleonitella vermicularis is the most modern species of the genus in the fossil record since other species were Palaeozoic. However, it is expected that the fossil record of the genus will increase and cover the gaps between fossil and present day charophytes bearing ecorticate thalli which are much like those described here.

Form-genus CHARAXIS Harris, 1939

Type species. *Charaxis durlstonense* Harris, 1939 from the Purbeck of Durlston (England), a lectotype proposed by Horn af Rantzien (1956).

Diagnosis. 'Vegetative charophyte organs agreeing in so far as they are known with *Chara*. Stem consisting of nodes and internodes, internode composed of a central cell surrounded by a ring of primary cortical cells which grow up and down from the nodes; and may cut off secondary cortical cells at their sides, primary cortical cells giving rise to spine cells. Leaves [branchlets] as in *Chara*, either corticated in the same way as the stem, or uncorticated' (Harris 1939, p. 67).

EXPLANATION OF PLATE 1

Figs 1–4. *Palaeonitella vermicularis* sp. nov.; LH-16100 (holotype). 1, partial view of thallus showing flexibility and variation in size; $\times 5$. 2, detail of thallus with ecorticate internodes; $\times 6$. 3, detail of thallus with branchlets preserved; $\times 6$. 4, detail of node showing about ten branchlet scars; $\times 30$.

Fig. 5. *Charaxis spicatus* sp. nov.; general view of LH-16110 (holotype); $\times 4$.



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Charaxis spicatus sp. nov.

Plate 1, figure 5; Plate 2, figures 1–9

Derivation of name. Name refers to the spike-like form of the thallus.*Holotype.* Specimen LH-16110 from the collection of Mr Armando Díaz-Romeral, Museo de Cuenca (Cuenca, Spain), deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.*Paratypes.* Thin sections LH-16105–LH-16109, housed in the same museum. These samples were taken from a dark grey laminated mudstone.*Type horizon and locality.* Second lithosome of finely laminated limestones of the La Huérguina Formation at Las Hoyas (Cuenca, Spain).*Material.* LH-16110, which is an apical fragment of thallus, is the only three-dimensionally preserved specimen found to date. LH-16121 is a rock sample containing several horizons rich in charophyte remains which supplied the slices to prepare thin sections LH-16105–LH-16109.*Diagnosis.* Thallus of *Charaxis* with nodes formed by six nodal cells bearing up to 18 ecorticate branchlets which are longer than the internodes above, completely covering them. Internodes several millimetres long and *c.* 1 mm wide formed by an internodal cell coated by first six then 18 cortical cells. Gyrogonites ellipsoidal ($400\text{--}530\text{ }\mu\text{m} \times 260\text{--}290\text{ }\mu\text{m}$), showing *c.* 16–18 circumvolutions and probably apical and basal necks.*Description**Description of three-dimensionally preserved specimen LH-16110.* Fragment of charophyte thallus bearing six large internodes (2.2–5.3 mm long and *c.* 1 mm wide) which are covered by vertical, non-spiralized cortical cells (Pl. 1, fig. 5). The preservation of this specimen does not allow a precise count of the number of cortical cells, which is, however, more than ten and less than 20. The five nodes preserved bear about 15 ecorticate, needle-like branchlets which are longer than the internode immediately above, covering it completely when not compressed. From this number of branchlets, which is similar to the most probable number of cortical cells, we deduce that the thallus was haplostichous, which means it had a cortex of primary cells only. Small scars at the base of nodes may correspond to bases of broken branchlets. No fructifications have been found attached to or in close association with this thallus.*Description of specimens from thin sections LH-16105–LH-16109.* These specimens are about the half of the size of LH-16110, but are identical to it in external morphology, number of branchlets and general cortication (Pl. 2, fig. 1). Therefore we consider that samples LH-16105 to LH-16110 belong to the same species. Internodes are formed by a large nodal cell ($200\text{--}330\text{ }\mu\text{m}$ in diameter) coated by small cortical cells (diameter $40\text{--}80\text{ }\mu\text{m}$). Close to the nodes there are six large cortical cells (Pl. 2, fig. 6). At variable but short distances from nodes, these cortical cells trifurcate: two small laterals and a larger central tube arise from each original cell (Pl. 2, figs 3–4). This larger central cell becomes smaller towards the distal part of the internode. As a result,

EXPLANATION OF PLATE 2

Figs 1–9. *Charaxis spicatus* sp. nov. 1, thin section LH-16105; longitudinal section of thallus; $\times 20$. 2, 7–8, thin section LH-16106. 2, longitudinal section through node showing insertion of three branchlets in each nodal cell (arrow); $\times 20$. 7, oblique sections through distal part of internodes; $\times 30$. 8, longitudinal section through fertile node showing three gyrogonites; $\times 20$. 3, thin section LH-16107; tangential section of node and subjacent internode showing cortical cells branching downwards (arrow); $\times 20$. 4, thin section LH-16108; longitudinal section through node and internode with secondary cortical cells formed by upwards branching of primary cortical cells (arrow); $\times 20$. 5–6, 9, thin section LH-16109. 5, transverse section through apical internodal cell and branchlets; $\times 30$. 6, transverse section through proximal part of internode showing primary and secondary cortical cells of different size; $\times 30$. 9, longitudinal section of gyrogonite; $\times 50$.



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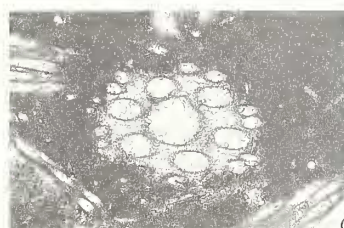
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close to the centre of an internode there are about 18 cortical cells of equal diameter, three per original cortical cell (Pl. 2, fig. 7). In the centre of the internode, cortical cells coming from adjacent nodes do not interdigitate since cortications with 36 cells were not found. Nodes are formed by six large globular cells, from which three ecorticate branchlets emerge (Pl. 2, fig. 2). As a result about 18 extremely long branchlets develop and appear to cover completely the next internode and node in an apical direction (Pl. 2, fig. 5). Taking into account that the number of branchlets equals the final number of cortical cells per node, the cortex of this species could be termed haplostichous. Gyrogonites have been found attached to certain nodes and are ellipsoidal ($400\text{--}530\text{ }\mu\text{m} \times 260\text{--}290\text{ }\mu\text{m}$) with an isopolarity index ($\text{height} \times 100/\text{diameter}$) of 104–108 and about 16–18 circumvolutions (Pl. 2, fig. 8). Several gyrogonites found in the same thin sections, which appear to belong to the same species, show apical and basal necks (Pl. 2, fig. 9).

Comparisons. The new species has approximately as many branchlets and cortical cells as the lectotype of the genus *Charaxis durlstonense* but differs in the absence of cortication in branchlets. According to Groves (1933), the Tertiary species *Charaxis blassiana* (Heer 1855) Harris, 1939 and *Charaxis gypsorum* (Saporta 1862) Harris, 1939 are also haplostichous, like *Charaxis spicatus* sp. nov. However, they differ from the new species by their reduced number of branchlets. Other *Charaxis* species considered by Harris (1939) are either different from the point of view of cortex organization or are insufficiently known. *Charaxis striatus* Peck, 1957 is known only from internodal fragments which appear to be coated by an extremely large number of cortical cells in comparison with the number of nodal cells or branchlets. Using this character it may be distinguished easily from the new species described here. Schudack (1989, 1993) suggested that *Charaxis striatus* should be included in the form genus *Munieria* Deecke, 1883, and may be synonymous with *Munieria grambasti* subsp. *sarda* Cherchi, Gušić, Schmidt and Schroeder, 1981, which he considers a Clavatoraceae. However, the genus *Munieria*, as originally defined by Deecke (1883), includes incompletely calcified vegetative remains which may correspond to several of the charophyte form-genera presently known.

Remarks. *Charaxis spicatus* is strongly reminiscent of thalli of extant *Chara*, which may justify the inclusion of the new species in Characeae. However, the presence of gyrogonites bearing apical necks in the same horizon (but not in anatomical connection with thalli) makes this attribution unsure. In the Lower Cretaceous, gyrogonites with apical necks are typical of the extinct family Clavatoraceae.

Form-genus CLAVATORAXIS gen. nov.

Derivation of name. From Clavatoraceae, the extinct charophyte family bearing this type of vegetative remains and *axis* (Latin).

Type species. *Clavatoraxis robustus* sp. nov.

Diagnosis. Verticillate thalli organized in nodes with branchlets separated by corticate internodes. Spine-cell rosettes are present at least in some parts of the thalli.

Remarks. The presence of spine-cell rosettes was first noticed on thalli of *Clavator reidii* by Harris (1939). However, Harris found fructifications attached to the silicified vegetative remains that he studied, enabling him to ascribe such remains to a taxon using the fructification-based systematics of fossil charophytes. The new form-genus *Clavatoraxis* is created for sterile clavatoracean verticillated vegetative remains which cannot be attributed to any species of fructification.

EXPLANATION OF PLATE 3

Clavatoraxis robustus gen. et sp. nov.; holotype, LH-16111; young portion of thallus; $\times 2.5$.



MARTÍN-CLOSAS and DIÉGUEZ, *Clavatoraxis*

Clavatoraxis robustus sp. nov.

Plate 3; Plate 4, figures 1–4; Plate 5, figures 1–9

Derivation of name. From its overall robust appearance, making it one of the largest and strongest thalli known from a Recent or fossil charophyte.

Holotype. Specimen LH-16111 from the collection of Mr Armando Díaz-Romeral, Museo de Cuenca (Cuenca, Spain), deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.

Paratypes. Specimens LH-16112–LH-16114 and thin sections LH-16116–LH-16120 housed in the same museum.

Type horizon and locality. Second lithosome of finely laminated limestones of the La Huérguina Formation at Las Hoyas (Cuenca, Spain).

Material. LH-450 A/B (portion of thallus), LH-823 A/B (portion of thallus), LH-1020 (portion of thallus), LH-1924 (small portion of thallus), LH-1941–LH-1943 (three small portions of branchlets in the same rock sample), LH-7087 (portion of thallus), LH-7361 (apical portion of thallus), LH-8016 (impression of portion of thallus), LH-8017 (portion of branched thallus), LH-8047 (impression of portion of thallus), LH-8114 (small portion of thallus), LH-8061 (portion of thallus), LH-13152 (portion of thallus with evidences of erosion), LH-13153 (impression of clavatoracean utricle), LH-13190 (portion of thallus with clavatoracean utricles scattered around), LH-13368 (portion of branchlet), LH-14114 (portion of thallus), LH-14180 (portion of thallus and impressions of utricles), LH-16111 (apical part of young thallus, holotype), LH-16112 (large mature thallus, paratype), LH-16113 (portion of mature thallus, paratype), LH-16114 (portion of mature thallus, paratype), LH-16115 (large sample with abundant fragments of thalli which supplied rock slices for thin sections), five thin sections (paratypes) LH-16116–LH-16120, LH-16122 (impression of two large portions of thalli and other smaller fragments).

Diagnosis. Several hundreds of millimetres long and 2–3 mm wide thalli of the *Clavatoraxis* type with first-order opposite branching and spine-cell rosettes completely covering internodes which are not terminal. In terminal, last order branchlets, spine cell rosettes are organized in nodes, separated by corticate, rosette-free internodes.

Description. Thalli supported by a main axis which is several hundreds of millimetres long and 2–3 mm wide, robust in overall appearance (Pl. 3). Branches attached to main axis are opposite and may further branch dichotomously or trichotomously (Pl. 3; Pl. 4, fig. 1). First and second order internodes are 16–44 mm long, spirally corticate (Pl. 5, fig. 1). Cortication formed by six cells near the nodes which interdigitate with the six cortical cells of an adjacent node giving the central part of an internode a 12-celled cortication (Pl. 5, figs 2–3). Internodes covered with spirally arranged, spine-cell rosettes, *c.* 0.5 mm in basal diameter (Pl. 4, fig. 2; Pl. 5, fig. 5). Up to 25 spiral rows of spine-cell rosettes are observed in lateral views of internodes of the main axis (Pl. 3). Spine-cell rosettes are hemispherical structures formed by a large number of club-shaped spine-cells, which are 200–250 μ m long (Pl. 5, fig. 6). The apical swelling of such clubs is spherical, *c.* 100 μ m in diameter and filled with sparite. As a result, the surface of a spine-cell rosette is covered by crystalline spheres. Club-shaped spine-cells radiate from the base of a rosette which is directly open to a cortical cell, leaving a gap in the cortical cell wall at the insertion point.

Last order branchlets organized in whorls of six are *c.* 3–4 mm long and formed by swollen nodes with short corticate internodes (Pl. 4, fig. 3). Nodes are formed by spine-cell rosettes with wedge-shaped (not club-shaped)

EXPLANATION OF PLATE 4

Figs 1–4. *Clavatoraxis robustus* gen. et sp. nov. 1, 3, paratype LH-16112. 1, mature portion of thallus showing opposite branching; $\times 1$. 3, detail, showing six branchlets per node; $\times 4$. 2, paratype LH-16113; young portion of thallus showing spiral arrangement of spine cell rosettes; $\times 2$. 4, detail of mature branchlets in paratype LH-16114; $\times 4.5$.



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spine cells, whereas internodes are rosette-free (Pl. 5, figs 7–8). Young, apical parts of thalli show closely packed last-order branchlets with nodes almost superimposed without leaving space for internodes. In the mature parts, last-order branchlets become loosely opened and their nodes are separated by short internodes. Since last order internodes are not covered by spine-cell rosettes, the cortication may be observed from the outside of thalli (Pl. 5, fig. 4). However, only the wall of cortical cells adjacent to the axis is calcified and this results in the fossil internode having a striated surface (Pl. 4, fig. 4).

No fructifications have yet been found attached to the thalli studied. The vegetative characters of *Clavator reidii* as described by Harris (1939) are largely like the last-order branchlets of thalli of *Clavatoraxis robustus* described here. This may be evidence that *Clavatoraxis robustus* bore fructifications of the clavatoroid type or even that it represents the vegetative remains of genus *Clavator*. However, this conclusion is not supported by the material studied, which only contains atopocharoid utricles dispersed in the sediment around the thalli. Such utricles are globular, bottle-shaped and do not present calcified gyrogonites (Pl. 5, fig. 9).

Comparisons. Young and closely packed, terminal branchlets of the thallus of *Clavatoraxis robustus* are similar in external appearance to *Munieria baconica* Deceke, 1883 as figured by Conrad and Radoičić (1971, fig. 4) and Bystrický (1976, pl. 4, fig. 7). Also, the mature, loosely packed terminal branchlets have a superficial similarity to *Munieria grambasti* Bystrický, 1976. However, our material differs by having the nodes of such branchlets formed by spine-cell rosettes whereas in the genus *Munieria* such nodes are devoid of rosettes and bear cylindrical cells.

Remarks. This is the most common charophyte found at Las Hoyas.

Clavatoraxis diaz-romerali sp. nov.

Text-figures 2A–C, 3A–D

Derivation of name. After Mr Armando Diaz-Romeral from Cuenca (Spain), in acknowledgement for collecting and making available the material upon which this study is based.

Holotype. Specimen LH-16123 from the collection of Mr Armando Díaz-Romeral, Museo de Cuenca (Cuenca, Spain), deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.

Paratype. Specimen LH-16101 and thin section LH-16124 prepared from the same sample (Museo de Cuenca).

Type horizon and locality. Second lithosome of finely laminated limestones of the La Huérguina Formation at Las Hoyas (Cuenca, Spain).

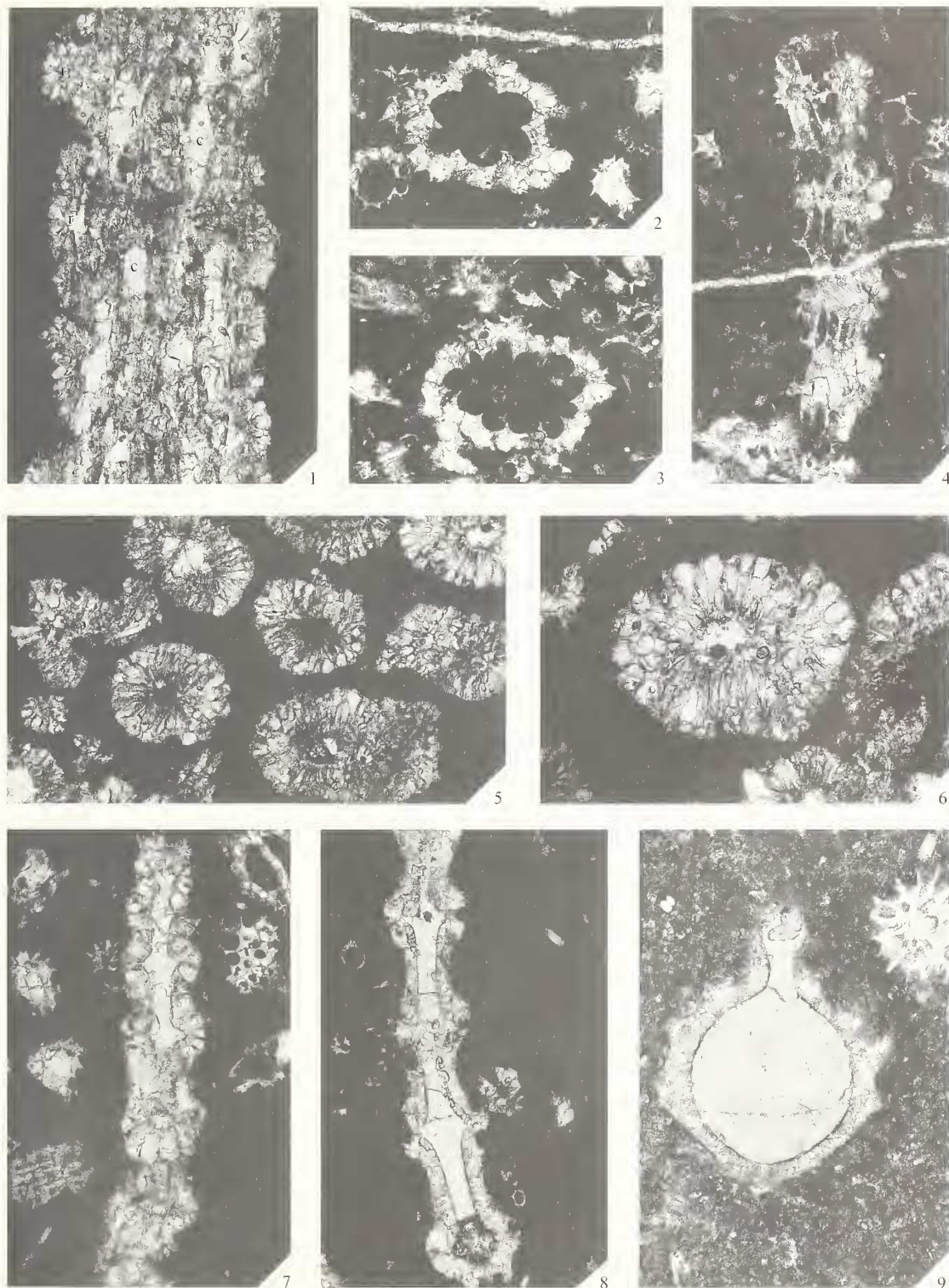
Material. Only the type material is known for this species.

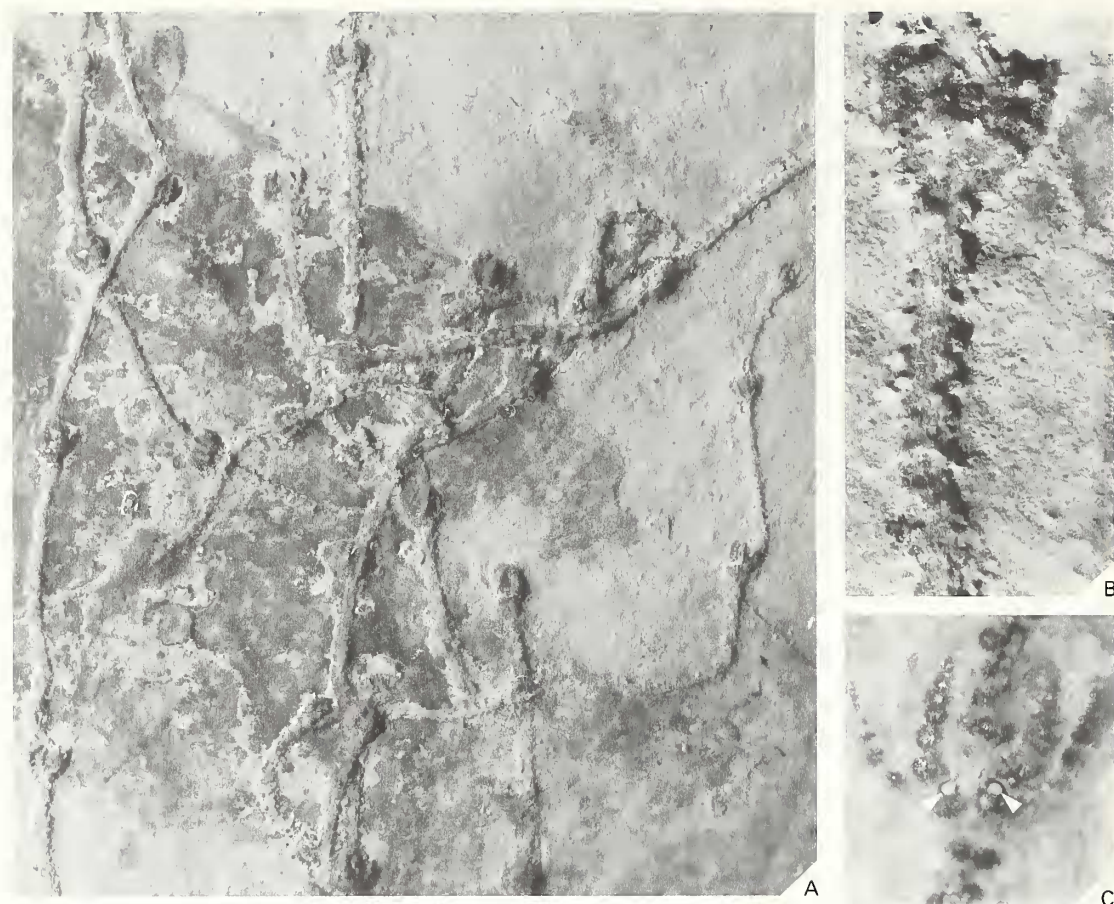
Diagnosis. Thallus of *Clavatoraxis* filiform and rigid in overall appearance. Nodes, separated by long internodes. Spine-cell rosettes small and formed by a reduced number of wedge-shaped calcite crystals are dispersed on the main axis leaving large bare areas.

Description. Thalli filamentous and rigid in overall appearance. Internodes corticate and extremely long in comparison with the size of nodes and branchlets (Text-fig. 2A). Each internode is 6.9–20.1 mm long and

EXPLANATION OF PLATE 5

Figs 1–9. *Clavatoraxis robustus* gen. et sp. nov.; thin sections of rock sample LH-16115. 1, thin section LH-16116; tangential section through thallus showing cortical cells (c) covered by spine cell rosettes (r); $\times 15$. 2, 7–8, thin section LH-16117. 2, transverse section through proximal part of internode. 7, oblique section of young branchlet. 8, longitudinal section of mature branchlet. All $\times 15$. 3–4, thin section LH-16118. 3, transverse section through distal part of internode; $\times 15$. 4, tangential section through branchlet; $\times 15$. 5–6, thin section LH-16119. 5, tangential section through surface of internode showing arrangement of spine-cell rosettes; $\times 15$. 6, detail of spine-cell rosette; $\times 25$. 9, thin section LH-16120; longitudinal section of atopocharoid utricle; $\times 30$.

MARTÍN-CLOSAS and DIÉGUEZ, *Clavatoraxis*



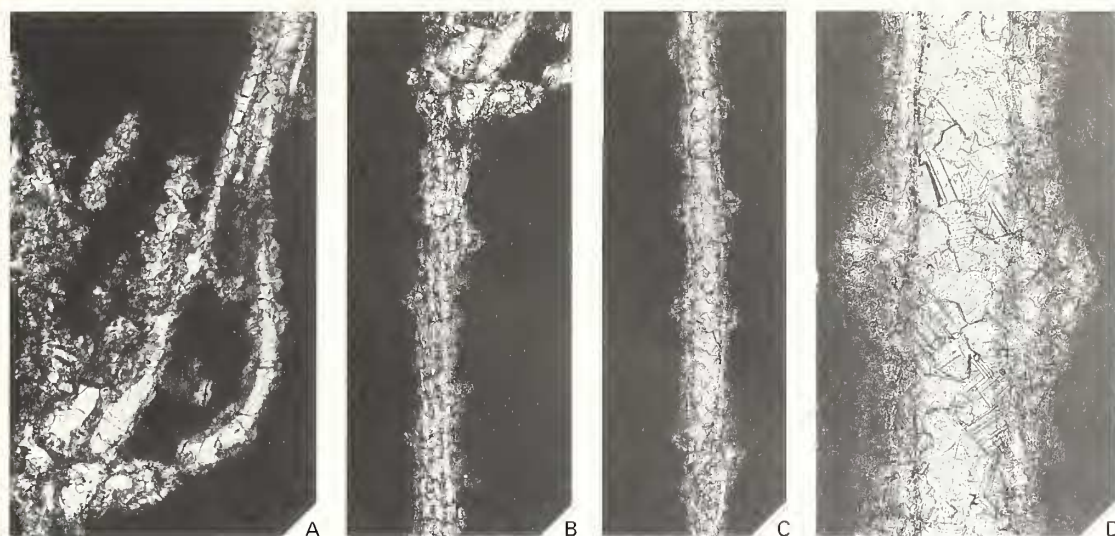
TEXT-FIG. 2. *Clavatoraxis diaz-romerali* sp. nov. A, LH-16123 (holotype); $\times 2.5$. B, detail of internode of holotype; $\times 5$. C, LH-16101 (paratype), detail of node bearing six branchlets (two cut off arrowed); $\times 15$.

0.7–0.9 mm wide. Corticate cells, thin (80–100 μm in diameter) almost vertical or only slightly spiralized (Text-fig. 3B). Internodal cell 180–230 μm in diameter. Spine-cell rosettes hemispherical or hemiellipsoidal, 135–350 μm in maximum basal diameter, formed by wedge-shaped cells, inserted in the internodal cells or in last order branchlets leaving a gap in the wall at the insertion point (Text-fig. 3D). Spine-cell rosettes are dispersed on internodes, leaving large bare areas between them (Text-fig. 3C). Nodes bear six short, 1.2–2.2 mm long, last order branchlets which are identical to last order branchlets of *Clavatoraxis robustus* (Text-figs 2C, 3A). They are covered by swollen spine-cell rosettes inserted at regular intervals (Text-fig. 2B). This gives a noded appearance to such last order branchlets.

No fructifications have been found associated with the thalli of this species, but from the presence of spine-cell rosettes we infer that they are clavatoraceans.

Comparisons. This species differs from *C. robustus* in its filamentous appearance and by bearing dispersed, rather than closely distributed, spine-cell rosettes. However, last order branchlets of the two species are identical. The cortication of this filamentous *Clavatoraxis* makes it easy to distinguish from other filamentous species of genus *Palaeonitella* which are ecorticate.

Remarks. This species is rather uncommon in the lacustrine laminites studied. It has only been found in two samples which contain abundant thalli preserved together and associated with



TEXT-FIG. 3. *Clavatoraxis diaz-romerali* sp. nov.; thin section LH-16124 of rock slice containing LH-16101. A, section through node; $\times 20$. B, tangential section through internode; $\times 15$. C, longitudinal section through internode; $\times 15$. D, detail of spine-cell rosettes; $\times 55$.

Palaeonitella vermicularis. This may indicate peculiar ecological conditions for this species of *Clavatoraxis*. Owing to the identical structure of last order branchlets in both species of *Clavatoraxis*, the hypothesis that they are merely ecotypes of the same biospecies cannot be ruled out.

COMPARISON WITH FRUCTIFICATIONS DISPERSED IN MARLY FACIES

This fossil assemblage of vegetative remains may be compared with the charophyte fructifications found dispersed in palustrine marly layers of the same age and formation underlying the site and described by Martín-Closas *in* Diéguez *et al.* (1995b). Marly layers provide the material to carry out current research on fossil charophytes, after sieving and sorting the calcified fructifications. In such palustrine facies, charophyte fructifications belong overwhelmingly to Clavatoraceae Atopocharoidae, and particularly to *Atopochara trivolis* var. *triquetra* (Grambast 1968) Martín-Closas, 1996. Less common are Clavatoraceae Clavatoroidae such as *Clavator harrisii* Peck, 1941 and *Asciidiella cruciata* (Grambast 1969) Schudack, 1993 and only certain samples are enriched with the atopocharoidean *Globator maillardii* var. *trochiliscoides* (Grambast 1966) Martín Closas, 1996 and the characean *Mesochara harrisii* Mädlér, 1952. These results correlate well with the relative abundance of *Clavatoraxis robustus*, vegetative remains probably related to Clavatoraceae Pia, 1927. Also, the rareness of *Charaxis spicatus* in the finely laminated limestones matches well the rarity of *Mesochara harrisii* in the laevigated marls if the affinity of *Charaxis* with Characeae Richard ex C. A. Agardh, 1824 is admitted. This is of special interest to palaeocharologists who, until now, have been unable to determine if the relative abundances of fossil fructifications reflect similar abundances of vegetative parts. However, there is also an inconsistency in the correlation of assemblages from different lithofacies. Nitellaceae Martín-Closas and Schudack, 1991 are not represented in assemblages of fructifications from marls whereas they may be represented by vegetative remains of *Palaeonitella vermicularis* if the affinity of the form-genus *Palaeonitella* with Nitellaceae Martín-Closas and Schudack, 1991 is accepted. This may be attributed to different ecological conditions during deposition of the lacustrine limestones and palustrine marls, but is most probably related to the slight calcification of reproductive remains of most Nitellaceae. The

lack of calcification of their gyrogonites, which accounts for their poor fossil record, is well documented in the charophyte literature (Feist and Brouwers 1990).

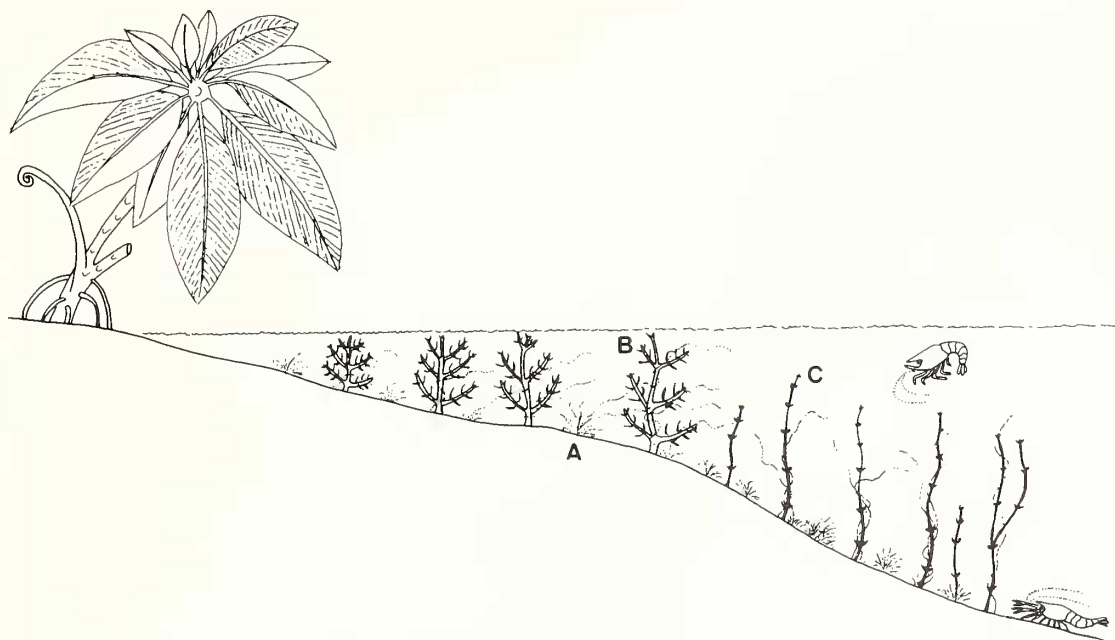
TAPHONOMY AND PALAEOECOLOGY

All charophyte vegetative remains found at Las Hoyas are preserved in calcite, unlike other whole remains of Lower Cretaceous charophytes (Harris 1939; Peck 1957; Musacchio 1971), which are silicified. The preservation in calcite accounts for the slight epidiagenetic corrosion which has obliterated some details of the surface of the thalli and of fructifications dispersed on the same rock samples containing thalli. From the point of view of biostratigraphy the charophyte assemblage is parautochthonous. The fragility of the preserved vegetative structures and their high degree of connection, along with the absence of rootlets, indicate that only slight translocation occurred before deposition. This enables reconstruction of the composition and structure of the ancient charophyte community.

Extant charophyte communities display vertical zonation according to the adaptation of species to different light intensities, whereas horizontal zonations are strongly influenced by competition with angiosperms and by different tolerances to salinity and water level fluctuations (Corillion 1957). For the Early Cretaceous, horizontal zonations have been proposed based on the association of charophyte fructifications with the remains of other organisms, such as ostracodes or foraminifers, which are salinity markers (Schudack 1993). Vertical zonations have not yet been attempted since almost nothing was known about the adaptive morphology of fossil charophyte thalli and the relative abundances of the thalli that produce the fructifications usually found dispersed in the sediments. This is now possible with the material studied (Text-fig. 4). *Clavatoraxis robustus* is the most abundant taxon. It possessed a strong, self-supporting structure as deduced from the rigidity given by its large, branching and corticate thalli reinforced with a coat of spine-cell rosettes. In extant *Chara*, spine-cell rosettes have been interpreted as protective elements against herbivory. Amphipods, aquatic coleoptera and crayfish are significant charophyte grazers in permanent shallow water lakes and ponds (Proctor 1996). Thus, *Clavatoraxis robustus* probably lived in permanent shallow lacustrine facies, forming a dense framework of interconnected thalli, as do some extant associations dominated by robust *Chara*. *Clavatoraxis diaz-romerali*, although filamentous in overall appearance, was also rigid as demonstrated by its fracturation in long, straight fragments. These thalli probably stood upright at the bottom of the lake. The extremely long internodes of *Clavatoraxis diaz-romerali* are reminiscent of a similar adaptation we have observed in extant *Chara* when subjected to low light intensities. Also, the open distribution of spine-cell rosettes may indicate low grazing pressure, which is typical of deeper lacustrine facies (Proctor 1996). From these observations we deduce that *Clavatoraxis diaz-romerali* occurred in light-limited, probably deeper, habitats in comparison with *Clavatoraxis robustus*. This would also explain why the two taxa are not found in association. *Palaeonitella vermicularis* is a relatively common taxon in the charophyte associations studied. Its filamentous and flexible thalli were found twisted round thalli of both *Clavatoraxis* species. This does not indicate only a close ecological relationship between *Palaeonitella* and *Clavatoraxis* in the lake of Las Hoyas but also that *Palaeonitella vermicularis* was unable to stand upright in the bottom of the lake without the support of other plants. Thus, as in some recent associations containing *Nitella*, *Palaeonitella vermicularis* would have formed less-organized thickets that grew supported by the framework given by other charophytes, particularly *Clavatoraxis*. The palaeoecological role of *Charaxis spicatus* is not known, due to its scarcity in the fossil assemblage studied.

FRESHWATER PLANT COMMUNITY EVOLUTION

Charophytes are the only subaquatic macrophytes found in the palaeolake of Las Hoyas after ten years of systematic collection and study of large remains (both carbonaceous and calcitic) and palynomorphs. Plant remains other than charophytes, although abundant and well preserved, have been attributed to groups of land plants which occurred in subaerial habitats (Diéguez *et al.* 1995b).



TEXT-FIG. 4. Proposed zonation of charophytes in the palaeolake of Las Hoyas. Near-shore associations were dominated by *Palaeonitella vermicularis* (A) and *Clavatoraxis robustus* (B) whereas in deeper facies the latter species was replaced by *Clavatoraxis diaz-romerali* (C). The tree-fern represented at the shore is *Weichselia reticulata*, one of the most abundant plants in Las Hoyas. Crayfish represented are *Delclosia martinelli*, a nektonic species and *Pseudastacus llopsi*, a benthic species which probably lived in association with charophytes.

The presence of a well structured and diverse charophyte community dominating the subaquatic environment in palustrine and lacustrine facies around the Barremian-Aptian boundary, along with the absence of other freshwater macrophytes, undermines current ideas on freshwater plant community evolution. To date it has been generally understood that 'aquatic pteridophytes may have... occupied many of the aquatic niches prior to angiosperm diversification', which occurred at the end of the Early Cretaceous (Collinson 1988, p. 326). This idea was based solely on the study of vascular plant remains. Although freshwater fern megaspores, particularly from *Azolla*, have been recorded in some Lower Cretaceous localities (Collinson 1980) they are far from being as abundant as charophyte fructifications. Besides this, freshwater ferns, which are small floating plants, have never been demonstrated to represent a serious competitor of charophytes. On the basis of evidence presented here we are now able to propose that before the radiation of freshwater angiosperms, continental subaquatic habitats were occupied extensively by well structured communities of charophytes in the absence of subaquatic embryophytes, whereas floating aquatic ferns were present only at certain localities. This hypothesis was suggested from the study of fossil charophyte fructifications by Martín-Closas and Serra-Kiel (1991) and is now supported by data from the fossil record of whole plant remains from Las Hoyas. The significance of subaquatic macrophytes for animal ecology is proposed to falsify this hypothesis. If charophytes were not the dominant macrophytes at Las Hoyas, benthic habitats would have remained devoid of any macrophytic vegetation, owing to the absence of subaquatic embryophytes during the whole Palaeozoic and early Mesozoic until the diversification of angiosperms. However, this is an untenable hypothesis, since huge populations of the crayfish *Pseudastacus llopsi* Via, 1971 were found at Las Hoyas, indicating that a significant macrophytic biomass existed to support them (Rabadà 1993). Extant astacid crayfish feed not only on macrophytes but also need a dense

macrophyte cover in which to shelter (Hobbs III 1991). The need for significant macrophytic cover formed by charophytes has also been given as an explanation for the development of particular groups of aquatic insects during the Early Cretaceous (Ponomarenko and Popov 1980).

A consequence of this conclusion is that freshwater vegetation remained extremely conservative during plant evolution. Charophytes, which are considered to be among land plant ancestors (Kenrick 1994), appear to have dominated the subaquatic macrophytic vegetation from the late Silurian, when they are first recorded (Ishchenko and Ishchenko 1982), until the radiation of subaquatic angiosperms, which occurred by the end of the Early Cretaceous (Mai 1985).

CONCLUSIONS

Four charophyte species, preserved as large plant remains, are described from the palaeontological site of Las Hoyas (Lower Cretaceous of the Iberian Ranges, Spain). A new genus (*Clavatoraxis*) has been created to include fossil vegetative remains related to Clavatoraceae. This genus includes two new species, *Clavatoraxis robustus* sp. nov. and *C. diaz-romerali* sp. nov. The other species are *Charaxis spicatus* sp. nov., probably related to fossil Characeae, and *Palaeonitella vermicularis* sp. nov., perhaps related to fossil Nitellaceae.

The abundance of taxa represented in the vegetative remains of charophytes found at Las Hoyas correlates well, at the family level, with the corresponding abundance of calcified fructifications found dispersed in sediments in the same formation.

The freshwater plant community of Las Hoyas was dominated by charophytes. *Clavatoraxis robustus* was the most abundant species and formed dense populations in the near-shore facies of the lake. *Clavatoraxis diaz-romerali* lived in deeper environments. Both species were associated with the filamentous *Palaeonitella vermicularis*, which was supported by other charophyte thalli.

Charophytes were the only subaquatic macrophytes of Las Hoyas, in the absence of submerged embriophytic macrophytes. This appears to indicate that submerged plant communities were dominated by charophytes until the radiation of subaquatic angiosperms, i.e. during most of the Palaeozoic and Mesozoic.

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